Invertebrate herbivores induce saxitoxin production in *Lyngbya wollei*

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Introduction

Most studies of freshwater benthic algal communities have attributed changes in community composition to anthropogenic eutrophication, even though selective herbivory can influence community structure by removing palatable species. The benthic community of Lake Guntersville, AL, USA is dominated by the cyanobacterium *Lyngbya (Plectonema) wollei*, but also includes the green alga *Rhizoclonium hieroglyphicum* and a variety of invertebrate herbivores, such as snails (*Pleurocera annuliferum*) and amphipods (*Hyalella azteca*). The dominance of *L. wollei* in this community may be reinforced by the production of chemical defenses, including saxitoxin (STX).

Hypotheses

1. *L. wollei* is less palatable to snail and amphipod grazers than *R. hieroglyphicum*.
2. Herbivores decrease the growth rates of monocultures of *L. wollei*.
3. Herbivores induce the production of STX.
4. Increased STX concentrations are correlated with decreased *L. wollei* growth rates.

Methods

We used artificial foods to test the palatability of these primary producers to an herbivorous snail, *Pleurocera annuliferum*, and to an omnivorous amphipod, *Hyalella azteca*. For amphipods, we also examined the palatability of crude extracts of *L. wollei*, pure STX, and *L. wollei* sheath material. We grew 1 g monocultures of *L. wollei* to test whether snails, amphipods, and mechanical damage induce STX production. We grew 1, 2, and 3 g of *L. wollei* and *R. hieroglyphicum* in a response surface design to examine how snail herbivory and potential competitors impact STX production.

Results

Both snails and amphipods preferred *R. hieroglyphicum* over *L. wollei*. *L. wollei* crude extracts and pure STX stimulated amphipod feeding; amphipods were deterred by *L. wollei* sheath material. In monocultures, snail herbivory generated strong compensatory growth, while amphipod herbivory decreased *L. wollei* growth rates. Snail herbivory induced high concentrations of STX, but amphipod herbivory did not. In the response surface design, with low N:P ratios, increased STX concentrations were correlated with decreased relative growth rates, suggesting a cost of STX production. However, no trade-offs were observed in monocultures, with higher N:P ratios.

Conclusions

Our results indicate that invertebrate herbivores can strongly influence the composition of freshwater benthic algal communities and the production of cyanobacterial secondary metabolites. Since previous reports of STX production in *L. wollei* have documented a high variability in toxicity among locations, efforts to reduce toxicity should not only focus on reducing nutrient availability, but should also consider interactive effects of palatability, herbivory and competition. Trade-offs between *L. wollei* growth rates and saxitoxin production may depend on the relative supply of nitrogen and phosphorus. The dominance of *L. wollei* in aquatic communities may be maintained by both induced chemical defenses and strong compensatory growth.